# Seasonal cycles in the sonic muscles of the weakfish, *Cynoscion regalis*

**Martin A. Connaughton**
College of Marine Studies, University of Delaware
700 Pilottown Road, Lewes, Delaware 19958
Present address: UT-Houston Medical School, Laboratory for Neuroendocrinology, P.O. Box 20708, Houston, Texas 77225

**Malcolm H. Taylor**
School of Life and Health Sciences and College of Marine Studies
University of Delaware, Newark, Delaware 19716

**Abstract.**—Male weakfish, *Cynoscion regalis*, were collected from the southwest portion of Delaware Bay from April through September in 1990 and 1991. Morphometric measurements of the sonic muscles, testis size (gonadosomatic index, or GSI), and plasma androgen concentrations were recorded to obtain data on the seasonality of sonic muscle condition and its relationship with the timing of reproduction in this population. The sonic muscles were bilaterally symmetrical and showed no significant seasonal differences in length or width across both collecting periods. Sonic muscle thickness did change significantly across both collecting periods and there was a threefold increase in sonic muscle mass during the course of each collecting period. GSI and levels of both plasma testosterone and 11-ketotestosterone also varied significantly across both collecting seasons. Changes in sonic muscle mass followed but lagged one to three weeks behind the rise and fall in plasma androgen levels. Pertinent models of skeletal muscle hypertrophy and atrophy are discussed as is the possibility that increased sonic muscle mass during the spawning season may increase the reproductive fitness of male weakfish.

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Sound production is used by a number of teleost species during aggressive or defensive behaviors (Gray and Winn, 1961; Steinberg et al., 1965; Hawkins and Chapman, 1966; Horch and Salmon, 1973; Hawkins and Rasmussen, 1978), but the greatest volumes of sound produced by teleosts are associated with reproduction. A number of marine families including Batrachoididae (Gray and Winn, 1961; Fish, 1964), Blenniidae (Tavolga, 1958b), Gadidae (Hawkins and Rasmussen, 1978), Gobiidae (Tavolga, 1958a), Triglidae (Moulton, 1956), Sciaenidae (Hildebrand and Schroeder, 1928; Pearson, 1929; Burkenroad, 1931), Serranidae, and Scaridae (Lobel, 1992) produce sound during the spawning season. Choruses of these sounds are generally limited to the season and geographic area in which the species in question spawns (Fish and Cummings, 1972; Fine, 1978; Takemura et al., 1978; Mok and Gilmore, 1983; Saucier and Baltz, 1993).

Teleostean sound production is generally accomplished through one of three mechanisms: hydrodynamic sound production via movement through the water, stridulation of bony body parts, or the use of specialized drumming muscles. The latter two mechanisms are often amplified by sympathetic vibration of the swim bladder, especially in the case of the drumming or sonic muscles. The sonic muscles may be intrinsic or extrinsic to the swim bladder. Intrinsic sonic muscles originate and insert entirely on the swim bladder, and appear as a part of the swim bladder wall. Extrinsic sonic muscles, however, originate on the cranium, pectoral girdle, or lateral body wall musculature and insert on or near the swim bladder (Tavolga, 1964; Demski et al., 1973).

Male sciaenids produce a 'drumming' sound through the use of sexually dimorphic, extrinsic sonic muscles. The Atlantic croaker, *Micropogonias undulatus*, is the only member of this family in which the sonic muscles are found in both the male and female (Smith, 1905; Tower, 1908; Fish and Mowbray, 1970; Hill et al., 1987). The drumming behaviors of sciaenid species are primarily limited to the reproductive periods of these species (Fish and Cummings, 1972; Takemura et al., 1978; Mok and Gilmore, 1983; Saucier and Baltz, 1993). Male drumming in sciaenids is believed to play a role in the spawning behavior of these species (Pearson, 1929; Guest and Lasswell, 1978; Thomas[1]).

[1] D. L. Thomas. 1971. The early life history and ecology of six species of drum (Sciaenidae) in the lower Delaware River, a brackish tidal estuary. Ichthyological Associates, Delaware Progress Rep. 3 (Part III), 247 p.

The weakfish, *Cynoscion regalis*, is a sciaenid which spawns in bays and estuaries from North Carolina to Long Island, New York, during the spring and early summer (Welsh and Breder, 1923; Mercer, 1983). Merriner (1976) noted a change in the coloration of the sonic muscles in male weakfish that paralleled the changes in testis condition during the course of the year.

The purpose of the present study was to determine whether the condition of the sonic muscles of male weakfish changes seasonally. In particular, this study was designed to determine the extent of change, if any, in the morphometrics of the sonic muscles over the course of the spawning season and to observe these variations in relation to changes in testis condition and plasma androgen levels.

## Materials and methods

### Sample collection

Male weakfish were sampled near the mouth of the Delaware Bay (lat. 38°50.30'N, long. 075°12.92'W) and roughly 40 km north of this (39°11.98'N, 075°23.20'W). Field collections were made from May through September in 1990 and from April through September in 1991. Specimens were collected by means of anchored or drifting gill nets, hook and line, and otter trawl.

Immediately after capture of the fish, blood samples were taken with heparinized syringes from the hemal canal, posterior to the anal fin. The blood was then placed in heparinized microcentrifuge tubes and stored on ice. Samples were centrifuged at 2,000 × g, and the supernatant was removed and frozen at –80°C for determination of plasma testosterone and 11-ketotestosterone levels via radioimmunoassay (RIA). In 1991, blood sampling was preceded by milt collection to determine the number of ripe specimens. Any drumming behavior was also noted.

Autopsies of the specimens provided total length (TL), total weight (TW), testis weight, and morphometric measurements of the sonic muscles. Testis weight and total weight were used to calculate a gonadosomatic index (GSI=[total testis weight/total weight] × 100). Sonic muscle weight, width (anterior-posterior axis of the muscle), length (dorso-ventral axis of the muscle), and maximal thickness (cross-section of the muscle) were measured for both the right and left sonic muscles. Orientation of sonic muscle width and length measurements is based on the dorso-ventral orientation of the muscle fibers (Ono and Poss, 1982). The sonic muscle-somatic index (SMSI) was calculated as SMSI = [total sonic muscle weight/total weight × 100], and the results were expressed as a percentage of TW. Indices for sonic muscle width (SMWI), length (SMLI) and thickness (SMTI) were calculated as the mean of the measurement for the right and left sonic muscles/total length × 100 and were expressed as a percentage of TL. The color of the sonic muscles was also noted.

### Radioimmunoassays

Testosterone was measured by direct radioimmunoassay. Five µL aliquots of serum were placed in 2-mL conical glass tubes (methanol rinsed) and diluted to a total volume of 50 µL with borate buffer. Diluted samples were incubated at 60°C for one hour to dissociate the steroid from binding proteins. Standard solutions were prepared by dissolving crystalline testosterone (Sigma Chemical Co., St. Louis, MO) in absolute ethanol. Working standards (5, 10, 25, 50, 100, 250, 500 pg testosterone 5 $\mu L^{-1}$) were prepared in ethanol, dried to zero volume at 45°C under vacuum, and reconstituted in 50 µL of borate buffer. Standards and sample tubes were incubated with 100 µL (approximately 4,000 cpm) of dilute trace (1,2,6,7-$^3$H testosterone, cat. #NET-370, New England Nuclear Corporation) and 100 µL of reconstituted antiserum (Wein Laboratories, Succasunna, NJ) overnight at room temperature. Total counts were estimated by using vials containing 100 µL of dilute trace and 100 µL of saturated ammonium sulfate. Triplicate standard and serum samples incubated without the addition of antiserum were used to calculate nonspecific binding. Bound steroids were precipitated by adding 250 µL of saturated ammonium sulfate to each tube. The vials were centrifuged and 400 µL of the supernatant were removed and placed in counting vials along with 6 mL of scintillation cocktail. All tubes were shaken for 25 minutes, allowed to sit for at least one hour, and counted for 3–10 minutes in a liquid scintillation counter.

Testosterone measurements were assumed to estimate total testosterone levels, as the plasma was incubated at 60°C for one hour to dissociate any binding proteins in the plasma. The 11-ketotestosterone assay (Woods and Sullivan, 1993) measured only free, or unbound, steroid, as the protocol includes triplicate ethyl-ether extraction of unbound steroids from the plasma.

Cross-reactivities of the testosterone antiserum were ≥50% for 5α-dihydrotestosterone and δ-1-testosterone, approximately 18% and 12.5% for 5α-androsten-3β,17β-diol and δ-5-androsten-3β,17β-diol, respectively, and <5% for all other steroids tested (Wein Laboratories, Inc.). Tritiated 11-ketotestosterone and 11-ketotestosterone antiserum were gifts

from C. V. Sullivan (Dept. Zoology, North Carolina State University, Raleigh, North Carolina). This antiserum cross-reacted less than 2% with testosterone (Hourigan et al., 1991).

Extraction efficiencies for the 11-ketotestosterone assay, determined by extraction of samples spiked with a known amount of radiolabelled 11-ketotestosterone, were always greater than 85%. RIA parallelism was determined by measurement of various equivalents of plasma from a single plasma pool. The results were parallel to the standard curve over a range of 1–20 μL plasma for the testosterone assay and 25–250 μL plasma for the 11-ketotestosterone assay (sample sizes for the assays were 5 and 50 μL, respectively). When a range of steroid concentrations was added to plasma pool samples of known hormone concentration, the quantities of spiked steroid recovered were not significantly different from the quantities added for either assay. The intra- and inter-assay coefficients of variation were, respectively, 10.3% and 18.5% for the testosterone assay and 7.4% and 17.1% for the 11-ketotestosterone assay.

### Statistical analyses

Specimens with a TL outside a 15-cm range around the sample mean for each year were not included in this analysis. This limited size range was used for two reasons: first, to alleviate the possible effects of allometric growth on the indices used to present the data; and second, to remain within the size range of two- and three-year-old weakfish used by Villoso (1989). The calculated indices, such as GSI, were used only to display the data. Statistical analyses on testis weight and sonic muscle morphometric measurements were conducted by using analyses of covariance with TW or TL of the specimen considered as a covariate. Bilateral comparisons of sonic muscle morphometrics were made by using a paired *t*-test. Statistical analyses of plasma androgen levels were accomplished by using a one-way analysis of variance. The α level for these analyses was 0.05.

## Results

A difference was noted between 1990 and 1991 surface water temperatures, which rose more rapidly in 1991 (Fig. 1). Surface temperatures reached 26°C by late May in 1991 but not until late June in 1990. The apparent result of these temperature differences was a two-week difference in the course of events across the collecting period so that 1991 trends began earlier than those in 1990.

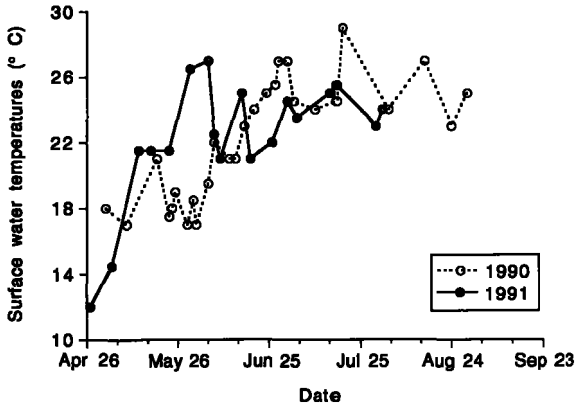


**Figure 1**

Surface water temperatures in the lower Delaware Bay for the 1990 and 1991 collecting seasons.

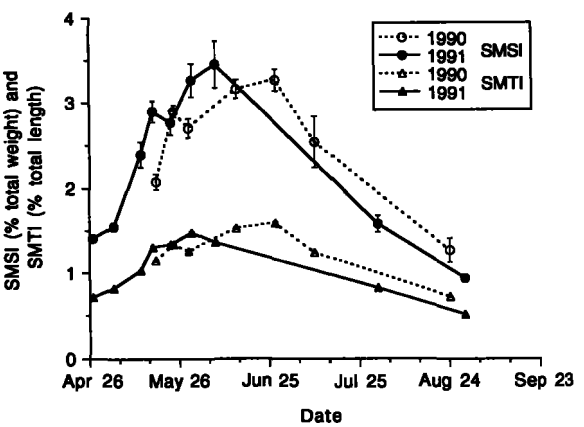


**Figure 2**

Sonic muscle thickness index (SMTI) and sonic muscle-somatic index (SMSI) of the weakfish, *Cynoscion regalis*, plotted across sampling date for the 1990 and 1991 collecting seasons. Points are means ($n$=3–10 fish) ± one standard error of the mean.

Sonic muscles were bilaterally symmetrical; we were unable to detect significant differences between the two sides in length, thickness, weight, or color in 1990 or 1991. Sonic muscle width on the left side was significantly longer than that on the right side in 1990, but this trend was not repeated in 1991.

Mean sonic muscle thickness changed significantly across the collecting season in both years. During both collecting periods, SMTI climbed to a peak of approximately 1.5% of TL by late June before steadily decreasing to post-spawning values of approximately 0.6% of TL (Fig. 2). Concurrently, there was a significant seasonal change in total sonic muscle weight in both 1990 and 1991. SMSI values rose to between

3.3 and 3.5% of TW by the peak of the spawning season in both years and decreased to roughly 1% of TW by the fall (Fig. 2). These seasonal changes in SMSI represent a threefold increase in sonic muscle mass.

Sonic muscle color also changed seasonally, following the changes in sonic muscle thickness. The sonic muscles were a dark blood-red throughout May and most of June. During late June and July muscle color faded to a dark pink, and in August to a light pink. During September and October sonic muscle color faded to a dark yellow and the muscle tissue became semitranslucent.

There were no significant seasonal changes in the mean sonic muscle length in either 1990 or 1991. SMLI values remained between 6 and 7% of TL across the entire collecting period during both years. A significant seasonal change in mean sonic muscle width was noted in 1990 but not in 1991. SMWI ranged from 28.6 to 30.8% of TL in 1990 and from only 28.3 to 29.2% of TL in 1991.

Total testis weight changed significantly across the collecting period in both 1990 and 1991. GSI values rose to a maximum of 4.2% of TW in both collecting seasons. After the peak of the spawning season, GSI values decreased rapidly, reaching postspawning lows between 0.1 and 0.2% of TW in the early fall (Fig. 3A).

Plasma androgen levels also varied significantly during both collecting seasons. Total plasma testosterone titers were somewhat lower in 1990, reaching a maximum of only 3.34 $ng \cdot mL^{-1}$, whereas 1991 values climbed to 5.5 $ng \cdot mL^{-1}$ (Fig. 3B). In both years levels decreased to postspawning values of between 1.2 and 1.6 $ng \cdot mL^{-1}$. Unbound plasma 11-ketotestosterone levels followed a trend similar to that noted for total plasma testosterone during both collecting periods (Fig. 3C). Maximal levels of unbound 11-ketotestosterone reached 1.1 $ng \cdot mL^{-1}$ in both years and then decreased to less than 0.1 $ng \cdot mL^{-1}$ by the fall.

Examination of weakfish in 1991 indicated that virtually all the specimens were capable of drumming when handled throughout the entire collecting period, regardless of changes in sonic muscle condition. Specimens produced milt throughout most of the study period, although no milt could be obtained before mid-May and none was obtained after mid-August.

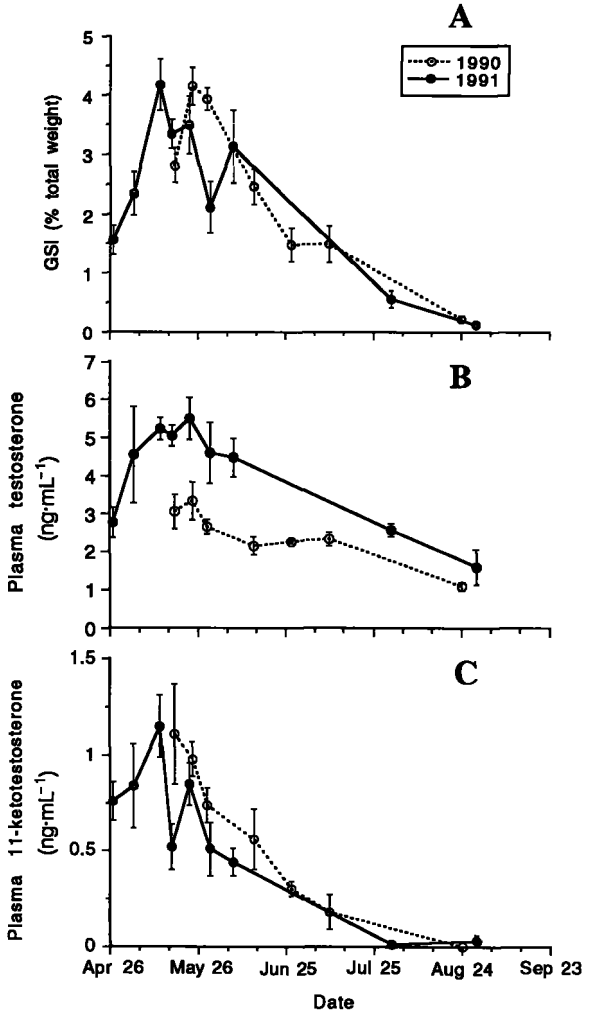


**Figure 3**

(**A**) Gonadosomatic index (GSI); (**B**) plasma testosterone concentration; (**C**) and unbound plasma 11-ketotestosterone concentration of the weakfish, *Cynoscion regalis*, plotted across sampling date for the 1990 and 1991 collecting seasons. Points are means ($n$=3–10 fish) ± one standard error of the mean.

## Discussion

The extreme seasonality of drumming activity in sciaenids (Fish and Cummings, 1972; Takemura et al., 1978; Mok and Gilmore, 1983; Saucier and Baltz, 1993) suggests that the condition of the sonic muscles in these species may not remain constant throughout the year. The data presented here indicate that the condition of the sonic muscles of weakfish does change seasonally; there was an approximate threefold difference in mass between the spawning and pre- or post-spawning periods. As the sonic muscle could not grow beyond its points of attachment (Tower, 1908; Ono and Poss, 1982), which define the length and width of the muscle, seasonal hypertrophy was expressed as an increase in muscle thickness. Seasonal changes in sonic muscle condition have not been documented in other sciaenids; how-

ever, a seasonal increase was noted in the sonic muscle mass of the male haddock, *Melanogrammus aeglefinus* (Templeman and Hodder, 1958). The sonic muscles of haddock are present in both sexes, but the seasonal increase in volume of the muscles was noted only in the males.

Maximal levels of total plasma testosterone observed in this study ranged between 3.5 and 5.5 $ng \cdot mL^{-1}$. Peak testosterone levels of 2.4 $ng \cdot mL^{-1}$ were noted in the closely related spotted seatrout, *Cynoscion nebulosus*.[2] Similarly, maximal levels of 11-ketotestosterone in the spotted seatrout fell between 8 $ng \cdot mL^{-1}$ and 10 $ng \cdot mL^{-1}$. Unbound 11-ketotestosterone levels in the weakfish, presumably expressing only a fraction of the entire plasma pool of this steroid, were roughly one order of magnitude less than maximal levels in spotted seatrout.

The similarity of the shapes of the androgen and SMSI curves suggests that plasma androgen levels may play a role in the seasonal cycling of the sonic muscle. Seasonal hypertrophy of the sonic muscles appears to be triggered by increasing plasma androgen levels in the spring. Similarly, the increased sonic muscle mass noted during the summer appears to be maintained by high plasma androgen titers. As androgen levels peaked and began to fall, sonic muscle mass continued to increase for a period of one to three weeks, then began to drop off as atrophy directly followed peak mass. There was no plateau in plasma androgen levels, nor was one noted in the plot of changing SMSI. Fine and Pennypacker (1986) noted an increase in the mass and a darkening in the coloration of the sonic muscles of male and female toadfish after gonadectomy and administration of either testosterone or 11-ketotestosterone. Injection of testosterone in male anurans can initiate calling behaviors and has been shown to accentuate the sexual dimorphism of the calling apparatus (Obert, 1977; Sassoon and Kelley, 1986).

In mammals, increased androgen levels can induce increased muscle protein synthesis and muscle glycogen storage, resulting in muscle hypertrophy (Lamb, 1975). Increasing the workload of a muscle can also result in hypertrophy of the muscle. Work-induced hypertrophy can occur in the absence of pituitary growth hormones, insulin, or androgens. Increased muscle mass in work-induced hypertrophy is the result of increased protein concentrations in the tissue. Much of this new protein is myofibrillar and is believed to result in increased cross-sectional area of the muscle fiber (Goldberg et al., 1975). Increases in muscle aerobic enzyme activities, mitochondrial protein concentrations, myoglobin concentrations, and muscle glycogen storage have been noted in exercise-induced hypertrophy in mammals (Holloszy, 1967; Edgerton et al., 1969; Barnard et al., 1970). It is possible that the hypertrophy experienced by the sonic muscles of weakfish in the spring may involve both of these pathways. Data presented here indicate that elevated plasma androgen levels may have played a role in the seasonal increase in mass noted in these muscles. Increasing androgen levels may play a direct anabolic role in muscle hypertrophy, or they may cue work-induced hypertrophy by initiating drumming behaviors, or both. Field hydrophone data from this population collected in 1992 (Connaughton and Taylor, in press) indicate that drumming activity begins approximately 4–6 weeks before maximal sonic muscle mass is reached.

The decreasing mass of the sonic muscles of weakfish in mid- to late-summer may be the result of decreasing androgen levels and decreased workload. Field recordings of voluntary drumming indicated that this behavior ceased abruptly after the spawning season (Connaughton and Taylor, in press). Atrophy caused by disuse in mammalian systems results in a decrease in fiber cross-sectional area and muscle mass (Desplanches et al., 1987; Musacchia et al., 1988). The decreased use of the sonic muscles after the spawning season might result in atrophy and subsequent weight loss in the sonic muscles.

Observations of specimens collected in 1991 suggested that while the sonic muscle condition declined throughout the summer and fall, the specimens were still capable of producing sound when handled. If the sonic muscles were capable of producing sound regardless of their condition, then the seasonal hypertrophy of these muscles must play a role other than activation of the muscles. Muscle hypertrophy in mammals can result in more powerful muscle contractions by that muscle (Goldberg et al., 1975). An increase in the strength of the sonic muscle contraction might increase the amplitude of the drumming call, allowing the male to be heard at greater distances or at increased intensities at a given distance, or both. Also, potential increases in aerobic capacity and in concentration of mitochondria may increase the stamina of the sonic muscles, permitting calling bouts of longer duration.

If male drumming plays a role in weakfish reproductive behavior, the condition of the sonic muscles may affect an individual's reproductive success. However, maintenance of peak condition of this other-

[2] P. Thomas, N. J. Brown, and C. R. Arnold. 1982. Seasonal variations of plasma androgens and gonad histology in male spotted seatrout, *Cynoscion regalis* (Family: Sciaenidae). *In* C. J. J Richter and H. J. T. Goos (eds.), Proceedings of the international symposium on reproductive physiology of fish, p. 111. Centre for Agricultural Publication and Documentation, Wageningen, Netherlands.

wise unused muscle throughout the remainder of the year might consume energy that could otherwise be budgeted toward growth, foraging, or predator avoidance and thus increase the individual's chances of reproducing again. Seasonal hypertrophy and atrophy of the sonic muscles ensure peak mass only at the appropriate time. This cycle is presumably driven by an indicator of the proximity of the spawning season, such as day length and correlated temperature changes, operating through changes in plasma androgen levels.

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